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DEVELOPMENTAL SELECTION IN VASCULAR PLANTS[1]

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(WITH TWENTY-EIGHT FIGURES)

In the numerous explanations and discussions of natural selection in the *Origin of species* and since the time of DARWIN, the process of competition has usually been regarded as taking place in the external environment. In striking contrast with this, developmental selection is characterized by the fact that it occurs between very minute or embryonic individuals whose struggle is limited to what might be termed an internal environment. It is well illustrated by the selection resulting from the polyembryony within the developing seeds of conifers and cycads, the embryonic selection in this case being a special form of developmental selection. The embryos of the latter are wholly surrounded by organic tissue; they are entirely inclosed within the ovule of the parent plant. Equivalent forms of developmental selection are found in ferns as well as in angiosperms, and it is intended to discuss briefly these internal selective processes in their relation to organic evolution.

Developmental selection is not to be confused with any of the older well known theories involving internal forms of selection. WEISMANN's germinal selection is described as an internal process, but this is a supposed struggle between biophores within the germ cells; it is not even a competition between individual cells, and can be imagined only. It is based on a speculative hypothesis

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entirely incapable of experimental proof. Likewise Roux's theory of intra-selection or the battle of the parts, a supposed struggle between the various organs of the body of a developing individual, is not a struggle between different individuals, but only between differentiating tissues and organs. Developmental selection, on the other hand, occurs between definite individuals which may be unicellular or multicellular, but the process is not intracellular. This can easily be demonstrated and is capable of being subjected to observation and experimental study.

The several isolation theories, as well as the other theories of species forming auxiliary to natural selection, have neglected any significant allusion to the type of illustrative material discussed in this paper. Developmental selection is different also from the theories of sexual isolation, physiological selection, or mechanical selection.

A definite rôle is not to be denied for natural selection, but it is not the only selective process. In developmental selection, we have a supplementary form of selection which occurs at other times during the life cycle, one which meets some of the most serious objections which have been raised against natural selection. It is capable of playing on mutations as well as other forms of variation, bringing about definite results in evolution. In fact, a real species forming rôle may be claimed for developmental selection, if we grant that such a rôle is to be found in any selective process. During the ontogeny of higher plants, therefore, there are a number of stages in the life cycle when a definite competitive selection between individuals occurs. In addition to natural selection, there is also this definite struggle between supernumerary gametophytes, when these are dependent on sporophytes, between supernumerary embryos as found in the polyembryony of gymnosperms and most ferns, or between excessive numbers of gametes.

In plants, natural selection, as it is ordinarily understood, occurs in the environment, when seeds or spores germinate in or on the soil, or when vegetative organs, such as roots, rhizomes, stolons, etc., from several neighboring plants of similar or different species give rise to new individuals in a crowded stand and in close competition. For animals, natural selection is usually understood to begin at birth, or when the young first come into contact with

the external environment.   That a selection may occur during the
earliest developmental stages of an individual, for instance, during
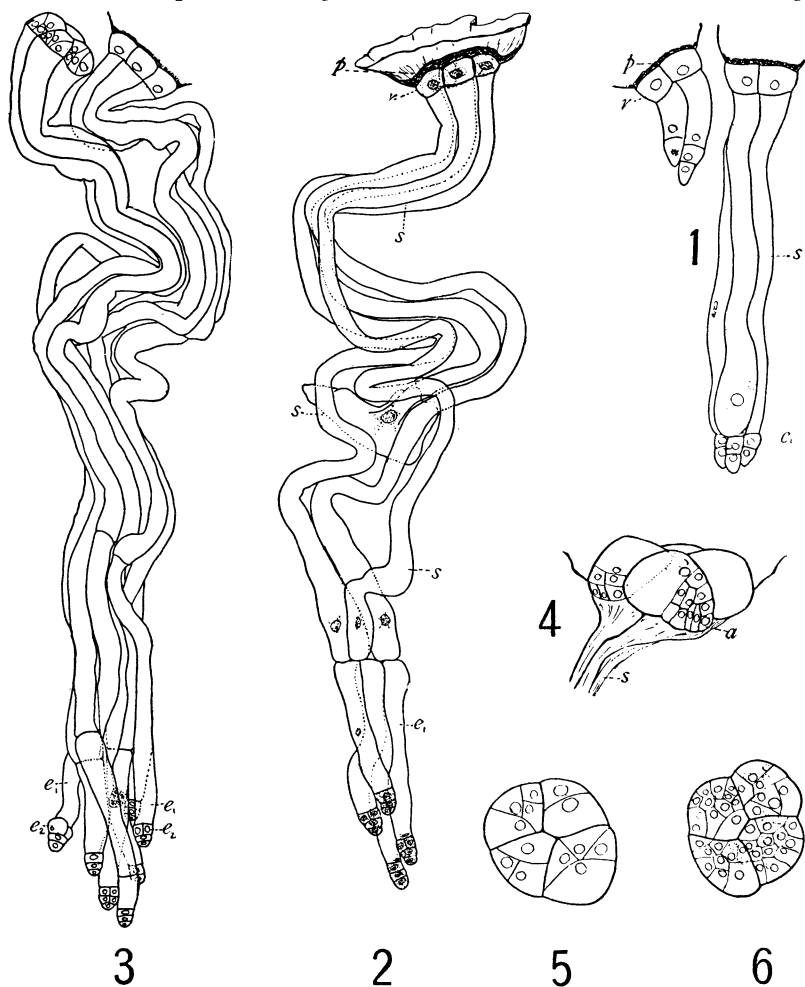
FIGS. 1–6.—Embryos of *Pinus Banksiana* showing embryonic selection: fig. 1,
two neighboring archegonia giving rise to embryos; fig. 2, system of eight embryos
and their suspensors (*s*, *e*) derived from single zygote by cleavage (rosette embryos [*r*]
still unicellular, but shown in later stages in figs. 4–6); fig. 3, two embryo systems
produced by fertilization of two neighboring archegonia, with sixteen embryos, eight
primary embryos (below), and eight rosette embryos (above), participating in the
competition.

the embryology or during the processes of seed development, is
an idea that apparently has not been considered seriously by

students of biology, judging from the general neglect of the subject of polyembryony in the literature of organic evolution. Many of the important facts concerned in the process of embryonic selection in gymnosperms, as the polyembryony of conifers and cycads, which have not been linked up with evolutionary doctrine, have been known to science for nearly a century.

Besides being entirely inclosed within the tissues of the parent plant, developmental selection is characterized by being intraspecific or reflexive. It is always a definite competition between similar individuals; usually it is between those of a single fraternity.

NATURAL SELECTION
Environmental process occurring in external physical and biological environment of organism, where conditions of struggle for existence are very complex

Struggle against unfavorable environment of physical surroundings.

Struggle against other species; extraspecific competition.

Struggle against fellows; intraspecific competition.

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Selection between vegetatively branching parts of either the gametophyte or sporophyte; buds and branches of trees, which later give rise to reproductive parts.

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DEVELOPMENTAL SELECTION
Occurring during early embryonic or gametophytic stages within tissues of parent plant, under conditions uniform for competing individuals

Interovular selection, between ovules within same ovary: (1) after fertilization, largely due to activities of contained embryos; (2) before fertilization, due in part to activities of contained female gametophytes, megaspores, or archesporial cells.

Embryonic selection, between embryos within the same ovule, or within tissues of parent gametophyte.

Gametophytic selection: (1) between male gametophytes, such as pollen tubes within carpellary and nucellar tissue; (2) between female gametophytes within the same ovule.

Gametic selection: (1) between male gametes or sperms; (2) between female gametes or eggs.

Although it is realized that in many instances this developmental process is influenced by external conditions, it is clear at least that the influence of these environmental conditions is very indirect, and that the highly complex external environment does not exert

a differential effect on the competing individuals. The foregoing outline is suggestive of the general relation of the several forms of developmental selection to the general process of natural selection.

Developmental selection expresses itself in some form or other in the sexual reproductive cycle of practically all vascular plants. It is probably also involved in the life cycle of most of the crypto-gamic forms, and is a factor to be reckoned with among animals as well. The main purpose in this discussion is to describe in a general way the various expressions of the principle of developmental selection as it applies to vascular plants.

The ordinary details of conifer embryogeny have been described (11) and may be assumed to be fairly well understood by botanists. It is generally known that in cycads or in such conifers as the spruce, for example, there are several embryos that engage in an intense life and death competition during their development. Only one embryo reaches its full term of growth to become the seed embryo, while the weaker individuals are aborted in the earlier stages. Only in extremely rare cases may two embryos be matured together in the conifer seed. In *Ginkgo* this happens rather more frequently, about 2 per cent of the seeds having been found with equally developed "twin" embryos (13). Even if several embryos should occur within the same testa, as in citrus seeds and several other angiosperms, these must necessarily come up so close together that a close competition between them will be inevitable after the seeds germinate. This competition which occurs after seeds germinate in the soil is environmental, however, and belongs to the categories of natural selection, where it remains as an intense intraspecific form of natural selection.

When pollination is successful enough to provide a plurality of male gametophytes, making polyembryony possible, practically all gymnosperms possess the feature of embryonic selection. Here the female gametophyte tissue is well formed before the embryos begin to develop, is somewhat firm and resistant, and it is only by a vigorous growth and rapid suspensor elongation, together with an abundant secretion of digestive ferments, that the successful embryo matures at the expense of its fellows and brings about their destruction. In angiosperms the endosperm within which the

embryo develops is much later in its origin, and is usually very soft and gelatinous in these early stages. This and the reduced suspensor of angiosperms may largely account for the fact that angiosperm polyembryony does not usually result in the definite selection of a single embryo before the seed is shed.

BROWN (1), who discovered polyembryony, pointed out that plurality of archegonia makes possible the fact of polyembryony among both cycads and conifers. It has been found also (5, 35) that in some conifers the zygote may undergo cleavage, resulting in several young embryos which compete with each other. Thus the fertilization of only one egg in *Pinus*, for example, results in the formation of eight embryos by cleavage (cleavage polyembryony), only one of which survives and completes its term of development (figs. 1–6). In other conifers, as in the spruce, the egg gives rise to only one embryo, but in any event the plurality of eggs makes possible simple polyembryony, in which a selection of embryos occurs.

A scheme of phylogeny, based in part on the character of polyembryony, whether simple or by cleavage, has been outlined in previous papers (5, 6). All the facts at hand seem to indicate that practically all conifers which do not possess cleavage polyembryony show structural evidence of having passed through this condition in their phylogeny. This indicates that either cleavage polyembryony originated among ferns, or it originated during the transition to the seed habit. All evidence is in favor of the latter alternative, and a definite hypothesis to account for the origin of cleavage polyembryony will be outlined in a later paper. In general, cleavage polyembryony is well developed among the more primitive conifers, and was eliminated sooner or later in all but one or two phyletic lines. Whether cycads passed through a similar stage of cleavage polyembryony is very uncertain. Nothing in the embryogeny of cycads thus far described appears to suggest this, but their simple polyembryony is doubtless of the same fern origin as that of conifers, that is, plurality of archegonia in the ferns from which cycads were derived.

Embryonic selection, either through cleavage polyembryony, plurality of archegonia, or a combination of both, is practically

universal among gymnosperms, and its character or type is of considerable importance in a study of phylogeny.   For the origin of simple polyembryony, we must turn to a study of pteridophytes, as it is very evident that the plurality of archegonia in gymnosperm gametophytes was derived from a similar plurality among their pteridophyte ancestors.

Embryonic selection among pteridophytes

Many living pteridophytes have simple polyembryony, that is, a plurality of young sporophytes growing on a single gametophyte. Whenever the number of these sporophytes greatly exceeds the ability of the gametophyte to nourish all of them through their period of embryonic development, so that some of them are starved out in their early stages, a selection must occur among them. If this selection takes place in the earliest stages, before these young sporophytes are exposed to the external environment and become independent, we have embryonic selection as truly as that found in gymnosperms.   When the several embryos in this competition are the result of a simultaneous fertilization, this embryonic selection has all of the advantages, as a measure of merit, that may be found in the gymnosperm polyembryony, and will be certain to result in the survival of the embryos that are strongest and most vigorous as determined by their actual performance.   The facts that are definitely known concerning polyembryony and embryonic selection in various groups of pteridophytes may be considered as follows.

LYCOPODIALES.—The occurrence of several embryos per gameto-phyte in *Lycopodium* was definitely reported and shown by BRUCH-MANN (3).   Figs. 7–9 definitely show this plurality of embryos. These embryos do not all mature, but some of them remain in an arrested but viable condition for a considerable period, and are able to resume their growth if the larger sporophytes are injured by drought or otherwise.   The smaller embryos probably fall into two groups, those which owe their origin to a fertilization simulta-neous with that forming the successful embryo, and those which originate by a subsequent fertilization.   It is very evident that the conditions for fertilization, even in these subterranean gameto-

phytes, are not continuous, but only occasional in occurrence. There is nothing that would hinder the fertilization of several or all of the archegonia which open on any occasion when fertilization takes place. A competition for food, together with a difference in the growth vigor of the embryos, probably determines which of several zygotes shall become the successful sporophyte. Some of the unsuccessful embryos doubtless abort and collapse in very
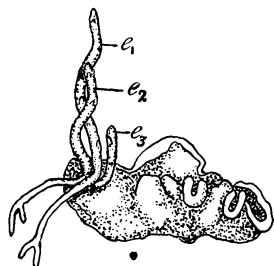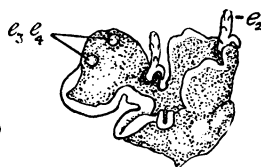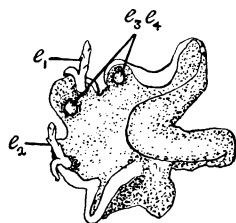

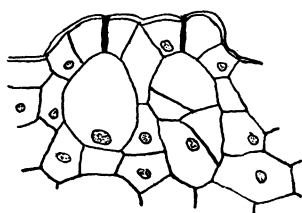
FIG. 7   FIG. 8   FIG. 9
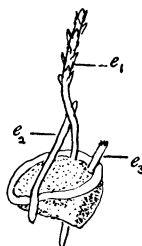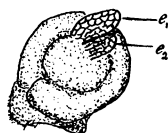
FIG. 10   FIG. 11   FIG. 12

FIGS. 7–12.—Fig. 7, gametophyte giving rise to several young sporophytes (e_1,e_2,e_3) of *Lycopodium annotinum*,×3; figs. 8, 9, gametophytes of *Lycopodium clavatum*, each with four embryos (e_1, e_2, e_3, e_4); after BRUCHMANN (3); fig. 10, section of gametophyte of *Tmesipteris* showing two neighboring embryos,×150; fig. 11, gametophyte of *Lycopodium volubile* bearing three sporophytes,×5; fig. 12, same with two very young sporophytes emerging,×8; figs. 10 and 11 after HOLLOWAY (23, 24); fig. 12 after CHAMBERLAIN (10).

early stages, soon becoming unrecognizable; while according to BRUCHMANN's accounts, confirmed by subsequent observers, many of them remain in an arrested but viable condition for some time. These may doubtless be added to by subsequent fertilization of still other archegonia. It appears that among some *Lycopodium* species with large gametophytes several full fledged sporophytes may be produced.

CHAMBERLAIN'S (10) description of several New Zealand *Lycopodium* gametophytes includes two instances among his figures showing a plurality of young sporophytes. His figure of *L. laterale* shows one sporophyte with protocorm and two protophylls, while a second embryo of much smaller size has just broken through the gametophytic tissue. *L. volubile* (fig. 12) is also shown with two young sporophytes, one nearly twice the size of the other.

HOLLOWAY (23, 24) has made an extensive study of New Zealand *Lycopodium* and *Tmesipteris* gametophytes, and has described a number of them. *Tmesipteris* has polyembryony, it is figured twice with two very young embryos, one of which is reproduced in fig. 10, and *Lycopodium* species are frequently shown with several sporophytes per gametophyte (fig. 11). From HOLLOWAY's letter, received in reply to an inquiry as to the occurrence of polyembryony among the New Zealand species of *Lycopodium* and *Tmesipteris*, the following paragraphs summing up these facts are taken:

I have examined a large number of prothalli of *Tmesipteris* (most of them externally only), and have observed that not a few (I cannot say how many) bore two and even three well grown young plants on the same prothallus. These plantlets were developing healthily, and presumably would all continue to do so as the prothallus decayed away. Probably, of course, the time would then come when they would begin to crowd each other out. . . . . In the prothalli which I sectioned, I found two instances in which two archegonia side by side had been fertilized and were continuing their development. On one of these prothalli there was also the remains of the foot of an older plantlet. No other embryos were to be seen on these prothalli. . . . . Again, there were several instances found in which two young embryos (more advanced than those mentioned in the last paragraph) were developing side by side, no more embryos being present on these prothalli.

The prothallus of *Tmesipteris* is of comparatively large size, and archegonia are present on most parts of it in great numbers, so that the examination of more prothalli in section should show that this form of polyembryony is by no·means uncommon. Also I have noticed that the prothallus can continue growing in size after a plantlet has become detached from it. . . . . I have examined a large number of prothalli of each of the following New Zealand species of *Lycopodium*, both externally and in serial sections: *L. cernuum*, *L. laterale*, *L. ramulosum*, *L. Billardieri*, *L. Billardieri gracile*, *L. varium*, *L. volubile*, *L. fastigiatum*, *L. scariosum*. I can give the following facts: The prothalli of the first named three (*L. cernuum*, *L. laterale*, *L. ramulosum*) are comparatively small and short-lived. I have never observed on any of them

more than one young plant or embryo in fertilized archegonium.   The pro-
thalli of the next named three (*L. Billardieri, L. Billardieri gracile, L. varium*)
are of the much branched epiphytic type, with a comparatively bulky central
region on which the sex organs are borne.   I have found that many well grown
prothalli in all three species have two and even three healthy plantlets.
Curiously enough, I have not found a single instance of two or more young
embryos or fertilized archegonia existing on the same prothallus, although I
have sectioned a large number.

The prothalli of the last named three (*L. volubile, L. fastigiatum, L. scari-
osum*) are large and deep living, the first two belonging to the *clavatum*
type and the third to the *complanatum* type.   I have examined a large number
of each of these both externally and in serial section.   These prothalli are of
course all comparatively large in size, and they frequently have two or three
developing healthy plantlets.   From serial sections I have found on one
prothallus of *L. volubile* one young plant and two embryos, and on another
four embryos.   The prothalli of *L. fastigiatum* supply the most noteworthy
instances of polyembryony.   One large prothallus showed no less than eleven
embryos in different stages of development and three young plantlets, all of
these fourteen being healthy.   Other prothalli showed from three to five
embryos.   The archegonia in these two species are nearly exclusively on the
liplike prominence· which surrounds the top of the prothallus, so that the
embryos and plantlets are generally quite close together.   In *L. scariosum*
I have also found two, three, and four embryos on the one prothallus.

From my own observations I can say that the large growing prothalli of
certain *Lycopodium* types (as enumerated above), and also those of *Tmesipteris*,
not uncommonly show polyembryony arising from the fertilization of several
archegonia.   I note, however, that CHAMBERLAIN shows two young plants on
a prothallium of *L. laterale* which is of the small-growing form.

It is very evident that *Tmesipteris* and some of the Lycopodiales
with large gametophytes may mature several sporophyte plants.
Doubtless some kind of embryonic selection is found even among
these, as it is highly probable that only a fraction of the zygotes
produced attain their full term of embryonic development.   Several
young sporophytes, however, are usually produced on various
parts of the tuberous gametophytes.   If these arrested embryos
remain healthy looking for a long period, a condition definitely
reported for some, this fact would indicate a more primitive
condition than that of their complete abortion.

Such a heterosperous form as *Selaginella* is much nearer to the
condition from which the seed habit was derived.   While some
large vigorous gametophytes of *Lycopodium* may frequently give

rise to several sporophytes of some size with or without embryonic selection, these smaller female gametophytes of *Selaginella* that are contained within the megaspore coats do not produce more than one maturing sporophyte. There are, however, a number of archegonia per gametophyte in *Selaginella*, and several figures have been published showing two or three embryos in the same section. One of these is PFEFFER'S well known illustration of *S. Mertensii* (fig. 13). When we consider the occasional character of fertilization and some of the difficulties that usually attend this event for a land plant, it is very probable that the fertilization producing these several embryos occurred simultaneously.

BRUCHMANN (2) states in his monograph on *S. spinulosa* that although several embryos may start to grow, but one comes to maturity. Miss LYON (31), in her paper on *Selaginella*, also shows several instances of polyembryony. The one shown in fig. 14 is given as a possible fertilization of two eggs in one archegonium, or of the fertilization

FIG. 13.—Female gametophyte of *Selaginella Mertensii* showing two embryos, ×160; after PFEFFER (33) as modified by GOEBEL (20).

of the ventral canal cell and egg. It is also possible that these embryos were derived from neighboring archegonia, as fig. 15 (drawn to the same scale as fig. 14) would seem to indicate, the embryos having digested the single layer of gametophytic cells that separated their venters. In any event, this shows polyembryony. These embryos are still so small that they are evidently formed from a simultaneous or nearly simultaneous fertilization, and one has already begun to grow a little faster than the other, indicating that embryonic selection is taking place. It appears at least that in some species of *Selaginella* embryonic
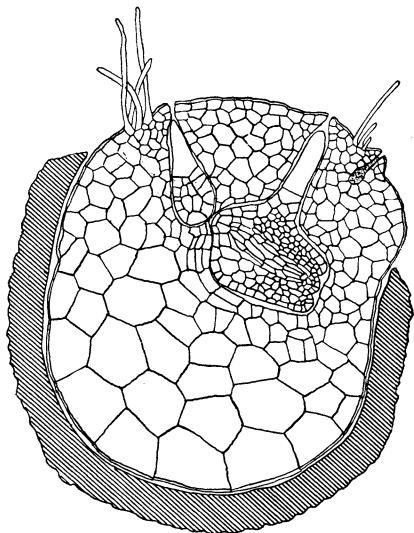
selection may play a definite rôle under normal circumstances. In *Isoetes* there are usually several archegonia, so that it is possible for several eggs to be fertilized, at least occasionally, but nothing has been recorded concerning an actual plurality of embryos.
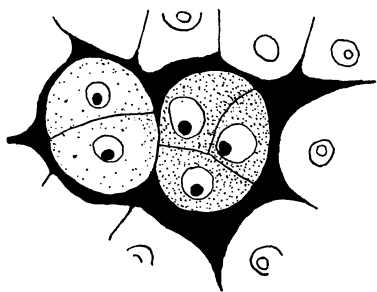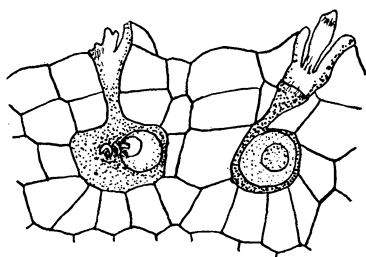

FIG. 14   FIG. 15

FIGS. 14, 15.—Embryos of *Selaginella apus* showing polyembryony; fig. 15, fertilization of egg in archegonium beside another zygote; fig. 14 may represent two zygotes of neighboring archegonia such as those in fig. 15 (drawn to same scale) after gametophytic tissue between them was digested away; after LYON (31).

EQUISETALES.—HOFMEISTER (22) definitely states that in *Equisetum arvense* the number of archegonia of a vigorous prothallium is from twenty to thirty. It exceeds, therefore, the number of antheridia of the largest male gametophytes. As a rule more than one egg is fertilized. He counted as many as seven embryos on one such gametophyte. Fig. 16 shows *E. arvense* with two neighboring archegonia containing embryos in competition. In a more recent study by KASHYAP (26) on *E. debile*, the author states that in these vigorous gametophytes the number of archegonia may reach two hundred or more. Although the prothallus may bear only a single sporophyte, eight to ten young sporophytes on a single gametophyte are said to be very common. Under conditions of laboratory culture KASHYAP obtained fifteen or more sporo-

FIG. 16.—Polyembryony in *Equisetum arvense;* after HOFMEISTER (22).

phytes on a single gametophyte (fig. 17). It is difficult to understand how only one or a few eggs could be fertilized where hundreds of archegonia are found, even if they are of successive origin. The result of such a fertilization would produce dozens or at least quite a number of zygotes, a majority of which never develop beyond the stage of only a few cells, and many probably succumb in the struggle for nourishment in the one-celled stage, or before they divide many times. *E. laevigatum* was recently
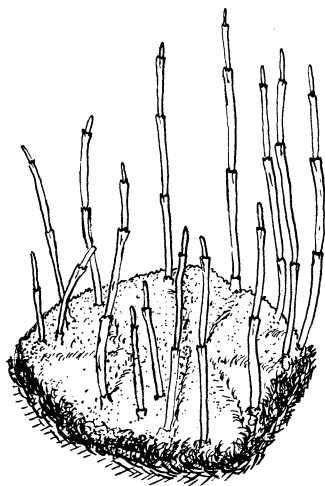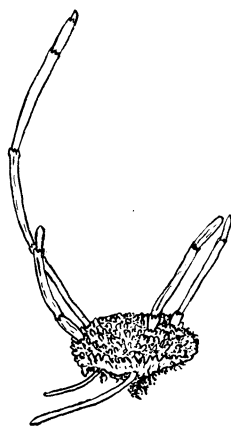
FIG. 17   FIG. 18

FIGS. 17, 18.—Fig. 17, gametophyte of *Equisetum debile* giving rise to fifteen sporophytes under laboratory culture,×1.5; after KASHYAP (26); fig. 18, *Equisetum laevigatum*, gametophyte bearing four sporophytes,×2; after WALKER (38).

investigated by Miss WALKER (38), and this species likewise has a plurality of young sporophytes, four being shown in one case (fig. 18), and six in another. It is evident that embryonic selection plays a rôle in most, if not all species of *Equisetum*. Plurality of embryos seems to have been found in all carefully investigated species.

OPHIOGLOSSALES.—In his work on the gametophyte of *Botrychium virginianum*, JEFFREY (25) states and gives illustrations of the fact that one frequently finds two or more sporophytes on a single prothallium. BRUCHMANN found many very young

embryos in *B. lunularia*, but stated that never more than two could develop on the small gametophyte.

In his studies of *Helminthostachys*, LANG (27) found a plurality of young sporophytes, and also found and described many small aborted embryos, whose arrest in various stages of development was due to the supremacy of the larger successful sporophyte. Figs. 19 and 20 are from his figures, made by combining several sections of the series, and show the existence of embryonic selection in *Helminthostachys*. He also gives habitat data which may be taken as evidence that the fertilizations which gave rise to the
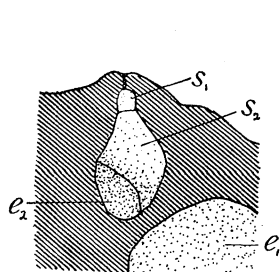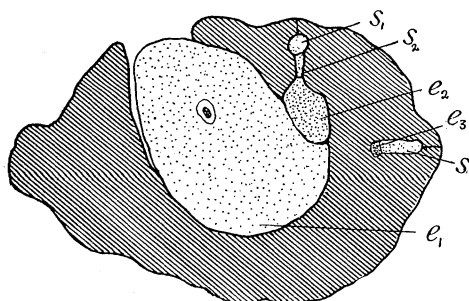
FIG. 19   FIG. 20

FIGS. 19, 20.—Fig. 19, arrested embryo (e_2) of *Helminthostachys* beside foot of larger embryo (e_1); after LANG (27); fig. 20, two arrested embryos (e_2, e_3) beside larger sporophyte (e_1); s_1, s_2, tiers of suspensor; reconstructed from serial photomicrographs by LANG (27).

withered arrested embryos occurred at about the same time as that of the successful sporophyte plant, and that the aborted embryos were starved by the more rapidly developing sporophytes.

Botrychium obliquum has been studied more recently by CAMPBELL (9). Something definite concerning the occurrence of embryonic selection may be inferred from this statement in the following passage:

Unicellular embryos are not uncommon, as several archegonia may be fertilized and begin to form embryos, but the later stages are not so easily found, and it was not possible to secure as complete a series as might have been wished. However, the essential points in the development of the embryos were made out, and there is no question as to the way in which the young sporophytes develop.

Of course embryonic selection would tend to make the later stages scarce, while the arrested unicellular and smaller embryos would be more frequent. Doubtless many of the latter are represented by the aborted embryos studied and mentioned by LANG and CAMPBELL.

LEPTOSPORANGIATE FILICALES.—Embryonic selection is also of common occurrence in many of the leptosporangiate ferns. In a paper on *Osmunda*, CAMPBELL (7) makes the statement, speaking of the *O. cinnamomea* gametophyte:

> Frequently more than one archegonium is fertilized as in the Gleicheniaceae (34), but as a rule only one embryo develops, although it is not at all uncommon to find several archegonia where the egg has evidently been fertilized, as is shown by its enlargement and investment with a cell wall. Only one case was met with where two larger embryos were present, but one of these was very much in advance of the other, and it is probable that the larger one would have ultimately starved out the other.

RAUWENHOFF (34) described the occurrence of several embryos in *Gleichenia* (fig. 22); and in *Vittoria* GOEBEL (19) found a similar
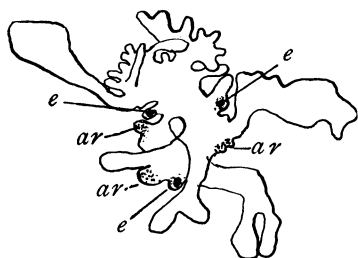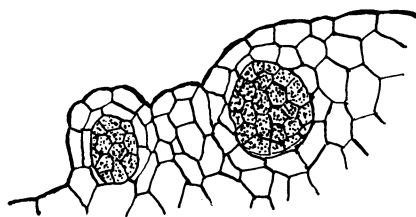
FIG. 21   FIG. 22

FIGS. 21, 22.—Fig. 21, gametophyte of *Vittoria* with three embryos (*e*) on various parts of branching thallus: *ar*, archegonia; after GOEBEL (19); fig. 22, embryos of *Gleichenia* showing polyembryony; after RAUWENHOFF (34).

plurality of sporophytes and embryos. He states that he has no doubt that several sporophytes may come from a single prothallium; at least he frequently noticed several embryos in various parts of the prothallium (fig. 21), also prothallia on which there were still other embryos in addition to the larger sporophyte. GOEBEL states that it is dependent upon circumstances of nourishment whether or not these smaller embryos continue their development.

Among other Filicales this feature of embryonic selection is likewise to be found. MARKLE has prepared many slides of fern embryos in order to supply them for school use, and is therefore able to speak from considerable experience. Most of his material, which includes a variety of leptosporangiate species, was obtained from greenhouses. He has found that by carefully examining his sections in the paraffin ribbons before fixing them to the slides, he has usually been able to make more than one good preparation showing a one-, a two-, or a four-celled embryo on a slide, out of the ribbon obtained from a single large gametophyte. MARKLE states in a letter:

> I do not think I have ever seen more than one embryo on a gametophyte where each had reached the stage with the first leaf evident. I have, however, seen a number of instances where there were at least two or three, possibly four embryos in the two-celled or four-celled stage on one gametophyte. In sectioning material in which the largest embryo was in the stage where the four quadrants have their respective primary organs (foot, root, stem, leaf) well organized, I have seen other small embryos, very evidently suffering from the competition and losing out in the fight with the larger embryos, as was shown by the shrunken appearance of the cells.

Among the fern gametophytes of the preceding discussion, there are quite a few instances in which the several embryos are only those of the somewhat independent or remote archegonial cushions. For example, *Angiopteris evecta* (fig. 23) and *Vittoria* (fig. 21) both have the young sporophytes some distance removed from each other. This condition is found among ferns having large or branching gametophytes, which may have several archegonial groups more or less remote from each other. Among these, as well as among the ferns with large tuberous gametophytes, there is active embryonic selection only when two or more neighboring archegonia are fertilized.

FIG. 23.—Gametophyte of *Angiopteris evecta* bearing two young sporophytes; after FARMER (18).

Likewise among leptosporangiate ferns the polyembryony has greatest significance when the competing embryos are near each other, as when they are on the same archegonial cushion. This form of embryonic selection, like that of conifers, only rarely produces

more than one sporophyte from a single gametophyte. This condition of polyembryony, which was casually mentioned by several students of pteridophytes, is well illustrated by fig. 24, which is a species of *Aspidium*, probably *A. Thelypteris*, collected in its natural habitat. While the larger embryo (fig. 24 *A*, e_1) has become multicellular, having approximately 25–30 cells, the second one (fig. 24 *B*, e_2), found on the remote side of the archegonial cushion, has remained unicellular, but has enlarged considerably.

Fig. 25 is from a gametophyte collected on the benches of a greenhouse whose species could not be determined, but could have been one of a half-dozen leptosporangiate species growing near by.
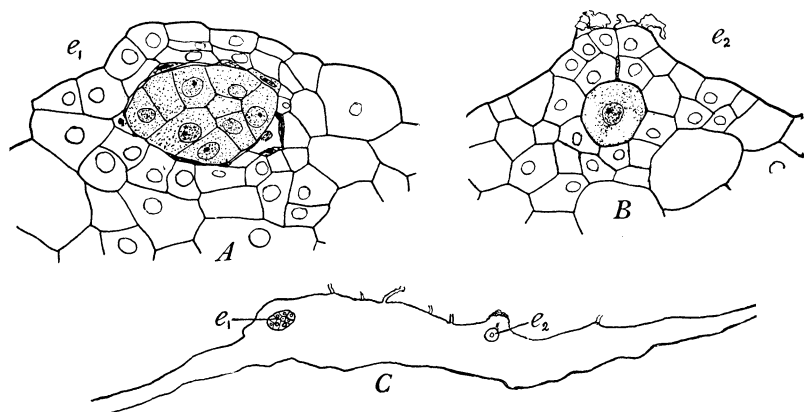
FIG. 24.—Embryonic selection in *Aspidium: A*, enlarged view of larger embryo of *C*, surrounded by calyptra; *B*, smaller unicellular embryo shown in *C* on same gametophyte, less than 1 mm. distant; (*C* reconstructed from several serial sections); *A* and *B*×200, *C*×42.

This is included here because it seems to show a stage slightly later than that of fig. 24, and indicates the fate of the smaller embryo of the latter. It is especially interesting to note the shrunken and starved appearance of the embryo in fig. 25 *B*. That the larger embryo starves the smaller is a very natural explanation; this is a factor which is very certain to be involved, but it is also possible that the excretions of one embryo tend to inhibit the development of the others. In ferns having large vigorous gametophytes with many archegonia, if the aborted embryos are not too quickly starved they should be subject to recall experimentally,

by any measures which would tend to prevent this embryonic competition.

From a careful examination of a number of species of leptosporangiate ferns, it is clear that there is a considerable period of enlargement of the egg following fertilization, before the zygote divides. It is obvious that the decisive part of the embryonic selection may transpire during this early period, so that most if not all of the zygotes are eliminated before they have undergone cleavage.

A few examples may be given showing the amount of increase in volume during the first stages of the embryogeny, calculated
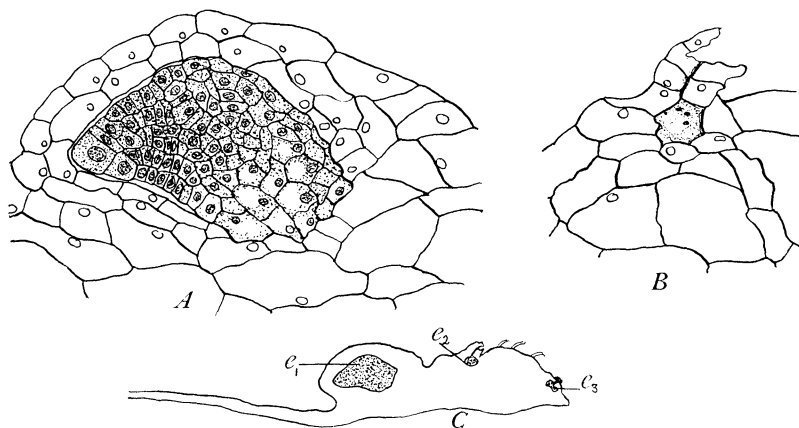
FIG. 25.—Fern gametophyte with several embryos in competition, representing slightly later stage than fig. 24; A is e_1 enlarged; B is e_2 (second unicellular embryo) with disintegrating nucleus, collapsing as it is aborted through embryonic competition; e_3 appears to be a third collapsed unicellular embryo (?); A and $B \times 200$, $C \times 42$.

from micrometer measurements. The average of several fertilized eggs in *Osmunda cinnamomea* measured 6000 cubic microns, while the zygote of the same species after only one cleavage measured 19,000 cubic microns. In *Adiantum* the diameter of the egg measured 17,000 cubic microns, while the two-celled zygote measured 65,000 cubic microns. In a species of *Pteris* the fertilized egg measured 33,000 cubic microns or less, while the two-celled zygote exceeded 195,000 cubic microns. Thus it appears that among leptosporangiate ferns there is a definite enlargement of the zygote of from 200 to 500 per cent during the first cleavages.

In eusporangiate ferns with well developed suspensors it is very much greater; hence the evidence to be found in the eliminated zygotes of this more active form of embryonic selection in ferns is not conspicuous. It occurs in the earliest stages, leaves only very small aborted embryos, and it is probably for this reason that embryonic selection has usually been overlooked as a normal process of the life cycle.

While many of the living ferns probably do not possess embryonic selection, at least as a very striking or prominent feature, practically all of them show good evidence of a derivation from forms possessing it; of having passed through this condition historically. During Paleozoic time, when pteridophytes constituted the dominant vegetation, embryonic selection was probably the prevailing condition. Even the environmental forms of competition were much more keen, as our vast coal deposits would indicate. There is little doubt that the early seed plants which were derived from these ferns retained embryonic selection, as it is a feature which has persisted until today in gymnosperms generally. The simple polyembryony of gymnosperms is therefore of fern origin.

SUPPRESSION OF EMBRYONIC SELECTION IN FERNS.—There are some pteridophytes among which there is a more or less complete elimination of embryonic selection. Such a highly specialized form as *Marsilia* presents a special variation in this direction, since only one archegonium is produced on the female gametophyte. Obviously there is no selection between two or more zygotes on the same prothallium. It appears that in *Marsilia* and other pteridophyte forms having only one archegonium, we have examples of the elimination of the embryonic selection, an advanced condition, doubtless the result of specialization. Leptosporangiate ferns, whose gametophytes are sometimes very much reduced in size, may perhaps provide additional interesting examples of the complete elimination of embryonic selection. Should this selection occur between archegonia, or between the eggs of neighboring archegonia during their development, it could certainly not be classified as embryonic selection; it may perhaps be designated as gametic selection, or in some other category of developmental selection.

It is needless to point out that morphological investigators have been concerned with only those stages in the development of the individual sporophyte or embryo which constitute the more important links of the life cycle, only occasionally illustrating or noting the occurrence of several embryos on one gametophyte. Sometimes an investigator illustrates a plurality of embryos without further comment, and LANG in his work on *Helmintho-stachys* reported a number of embryos only because he made use of the arrested embryos of one gametophyte in describing some of the missing stages of embryonic development.

STEPS IN EVOLUTION OF EMBRYONIC SELECTION AMONG PTERIDO-PHYTES.—If definite steps in the evolution of embryonic selection among pteridophytes are recognizable, these may serve as a rough measure of their phylogenetic position, at least of the relative position within each of the several well recognized groups. It would seem that at least the following stages or steps in the evolution of embryonic selection may be recognized.

1. Many sporophytes are found on one vigorous gametophyte, a large portion of which reach maturity. Selection may finally occur under conditions of crowding in early or later stages, but this elimination occurs largely in the environment, and must then be recognized as natural selection, as, for example, *Tmesipteris* and *Lycopodium* with large vigorous gametophytes.

2. A few sporophytes appear above the soil or break through the tissues of the gametophyte, but a selection occurs among a much larger number during their embryonic stages; arrested embryos remain turgid for a considerable period, as for example *Lycopodium*.

3. One or only very few sporophytes break through tissues of gametophytes, but a selection occurs among a large number in their embryonic stages; arrested embryos are soon aborted and not easily recognized, as, for example, *Equisetum, Helminthostachys*, and *Botrychium*.

4. Normally only one sporeling sporophyte is produced, but several archegonia are fertilized, and selection between zygotes occurs in early embryonic stages; arrested embryos are usually soon aborted and not easily recognized, as, for example, *Selaginella, Osmunda, Aspidium*, etc.

5. Gametophytes are so reduced in size that only one arche-gonium is produced, making selection between embryos of separate fertilization impossible, as, for example, *Marsilia* and *Pilularia*.

Selection between gametes

Among all of these pteridophytes another form of developmental selection may be recognized. Doubtless a selection occurs among the male gametes as they swim to the archegonia. That the archegonia attract the sperms chemotropically has long been known. The gametic selection is therefore a measure of their response to this stimulus. While it may be largely a matter of chance which of the many sperms that reach the archegonium and swarm about its neck actually reach the egg to effect the fertiliza-tion, there can be no doubt that the less active sperms or those otherwise defective would be eliminated in the race to reach the egg. If only the most vigorous sperms take part in fertilization, and there seems to be very good ground for this, certainly a form of gametic selection is to be recognized. It may be noted in passing that with its return to aquatic life, the natural sphere of swimming sperms, *Marsilia* has exchanged one form of developmental selection for another. Embryonic selection was made impossible and lost through reduction of archegonia, but gametic selection was doubt-less facilitated when this fern returned to the aquatic habit. Gametic selection is not a new suggestion, having been suggested by THOMSON (**36**) for animals, and it is probably in part along this line that the principle of developmental selection may be found to apply somewhat generally to the animal kingdom.

It must be remembered that no reduction divisions occur in the formation of sperms in ferns, nor is any special form of cell division known or recognized here which might bring about genetic changes. In animals the formation of sperms is accompanied by a chromatin reduction both equational and differential, a condition shared by some algae, notably *Fucus*.

OTHER FORMS OF DEVELOPMENTAL SELECTION.—There are still other forms of developmental selection which must be taken into account. One of these is illustrated by the selection which takes place at a certain stage of development in *Selaginella* between the

megaspore mother cells, a large number of which begin to appear only to degenerate when one of them is selected and enlarges to form the single tetrad of megaspores. This selection is neither embryonic, gametic, nor gametophytic, but belongs to a distinct category, somewhat similar to some other types of developmental selection which will be discussed later.

Developmental selection among spermatophytes

EMBRYONIC SELECTION.—Most striking of the forms of developmental selection of seed plants is the embryonic selection illustrated by the polyembryony of gymnosperms, which has already been described in a general way. The several embryos originating from the fertilized eggs engage in a competition in which the most vigorous individual is always the winner. Not only must the embryo rapidly become massive and multicellular, but it must also produce a stiffer and more vigorous suspensor, one which keeps the successful embryo in the commanding position. The winner is usually the foremost of the group of embryos, where the embryonal tubes of the elongating secondary suspensor are able to push the other competitors back, away from the most favorable position. This applies whether cleavage polyembryony occurs or not. The mature conifer seed has a single large embryo, but the remains of some of the other embryos participating in the competition can usually be found, crushed against the archegonial end of the embryonal cavity within the gametophyte (endosperm) by the suspensor or radical end of the successful embryo.

GAMETOPHYTIC SELECTION.—Another type of developmental selection is gametophytic selection. This is not intended to apply to the form of natural selection occurring between independent gametophytes, as those of liverworts or ferns, in the external environment, but rather to a plurality of male or female gametophytes which are dependent on a sporophyte, as they are in seed plants. It is well illustrated by the pollen tubes of a pine or other conifer whose competition predetermines in a measure which of the several archegonia shall first be fertilized. Although fertilization in conifers is almost simultaneous even in the various cones of the same tree, a fact first pointed out by HOFMEISTER (21), this

event does not usually occur absolutely simultaneously even in a single ovule. Some embryos are usually produced a little earlier than the others, and have a slight advantage, although this difference may represent only a few hours or minutes. The competition is continued between the several embryos in the ensuing embryonic selection, which becomes truly a struggle for existence, so that the resulting seed has only one embryo. Here in gymnosperms the developmental selection process is a sort of relay race between one pollen tube plus its embryo, and other pollen tubes plus their
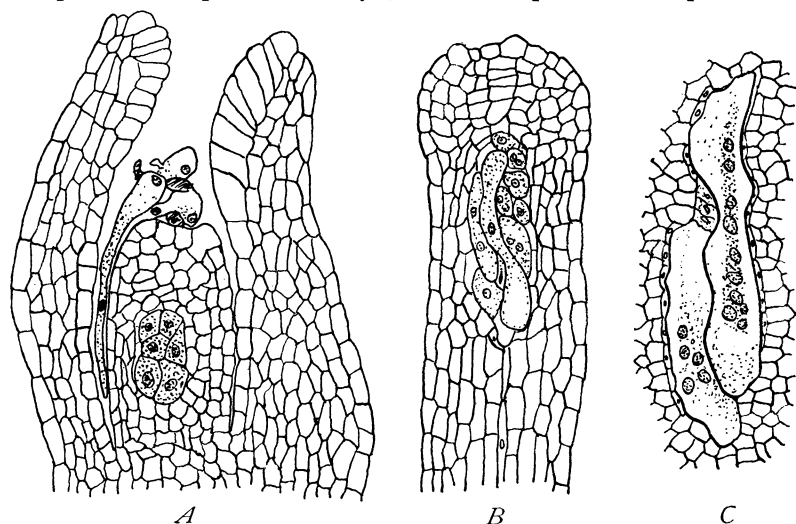
FIG. 26.—Sections of ovules of *Sequoia sempervirens*, showing selection between female gametophytes: *A*, ovule with six megaspore mother cells; *B*, numerous germinating megaspores; *C*, older stage showing two young gametophytes whose competition has persisted into multinuclear stage; after LAWSON (**28**).

embryos. The embryo of a gymnosperm seed is therefore the survival of a rapidly developing pollen tube combined with a very vigorous embryo.

Among conifers the male gametophytes are not the only individuals taking part in this competition. Female gametophytes may also undergo competition under normal conditions in some species. DUPLER (**16**), in his work on *Taxus canadensis*, showed that the existence of several female gametophytes arising from as many megaspores is quite the normal condition. LAWSON (**28**) found a similar situation in *Sequoia* (fig. 26), and apparently also

in *Cryptomeria* (**29**). The work of LOTSY (**30**) on *Gnetum* indicates the same thing, and occasionally slight evidences of this are found in *Pinus* and other conifers.

Even angiosperms sometimes have this competition between female gametophytes, which seems to occur as a functional form of developmental selection. This is especially true of some of the lower Archichlamydeae and Monocotyledons. *Casuarina* (**37**) has been reported to have as high as twenty or more megaspores, of which several enlarge considerably, but only one is functional. *Alchemilla* (**20**) has been observed with five or six ripe megaspores;
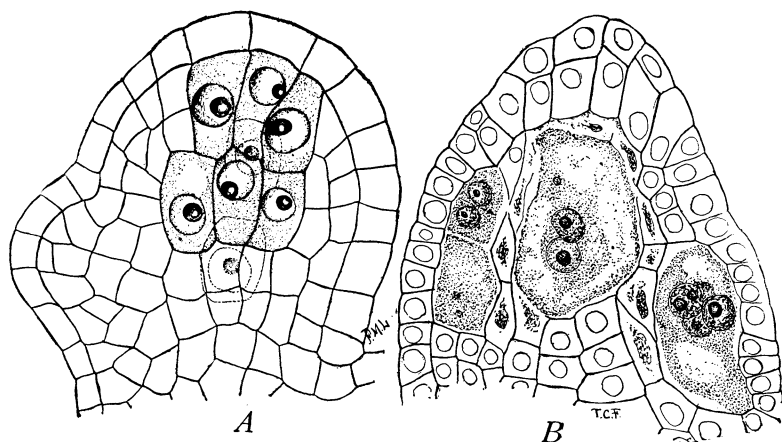
FIG. 27.—Selection between female gametophytes in *Ranunculus septentrionalis:* *A*, section of nucellus showing eight-celled archesporium; *B*, later stage showing several female gametophytes and aborting megaspores in early stages of development, ×400; after COULTER (**12**); cut lent by D. Appleton Company.

in *Arisaema* (**8**) something similar has been reported; and in *Ranunculus* COULTER (**12**) found as many as eight archesporial cells and three embryo sacs within the same ovule (fig. 27). Numerous additional examples are on record. GOEBEL (**20**), in discussing the many gametophytes of *Casuarina*, suggests that "biologically this repeats the case of the embryos of the Abietineae, where, of the many embryos which arise from one egg, only one develops." His interpretation of the significance of polyembryony in conifers is treated as a process of correlation, where he compares it to the

correlative "struggle" between vegetative parts, or flowers in a crowded inflorescence. It is evident that he recognized a significant similarity in these forms of developmental selection, although apparently he did not anticipate the significance of these facts in relation to the selective mechanism of evolution.

A very unique form of developmental selection is represented in *Welwitschia mirabilis* described by PEARSON (**32**). The female gametophyte gives rise to a number of nuclei, potentially eggs, which develop prothallial tubes that grow up into the nucellar tissue. When such a prothallial tube comes in contact with a pollen tube, fertilization takes place. The embryos may be found growing down through these prothallial tubes into the female gametophyte tissue. Although we have polyembryony, the selection is probably in part predetermined by priority of fertilization, which depends upon the pollen tubes and the prothallial tubes of the female gametophyte. Apparently the selection resolves itself, in part at least, into a competition between eggs, or prothallial tubes containing eggs, a form of selection between female gametes which is very rare in plants.

Megaspore tetrad formation and the abortion of the megaspores in angiosperms might suggest itself as a form of developmental selection, but the selection in this case seems to be largely one of position. It is not any megaspore of the group in a linear tetrad that may give rise to the embryo sac, but almost always the innermost of the four. This selection is not dependent on the physiological success of the megaspore, but is morphologically fixed, and therefore not properly included among processes of developmental selection.

Among angiosperms the selection between male gametophytes or pollen tubes represents the most important developmental selection machinery. In the pistil of the ordinary flower an excessive number of pollen grains may germinate on the stigmatic surface, but usually only a limited number of these can function in fertilizing the eggs within the ovules. Only one pollen tube is necessary to fertilize the single ovule in the pistil of maize, yet hundreds may fall on each stigma and germinate, producing pollen tubes of varying lengths. Fig. 28 represents the pistil of an

angiosperm, illustrating the important mechanism of this gameto-phytic selection.   A mature cotton boll contains an average of from 30 to 40 seeds, yet hundreds of pollen grains may germinate on the stigma of the pistil.   EAST (**17**) has deter-mined by actual count that there are usually 1200 to 2000 pollen tubes in a single pistil in tobacco, sufficient to fertilize from four to six times the number of ovules in the ovary.

Recent genetical studies have shown that this gametophytic selection in angiosperms represented by the pollen tubes has a signifi-cance of the first importance.   For example, CORRENS (**14, 15**) has shown that in *Melan-drium* there is a selection between the male gametophytes in their race to the ovules, that the female-producing pollen tubes are on an average decidedly faster in their growth than those carrying the factors which produce males.   By applying much pollen so as to crowd the pollen tubes, he was able to increase the pollen tube competition in favor of the production of more females, and by sparse pollination he was able to stay this competi-tion somewhat, resulting in the production of more males than under normal conditions. This may be taken as definite experimental proof of gametophytic selection in angio-sperms.

Experimental studies of pollen tube com-petition in angiosperms have been in progress for some time by the writer, and will be published in separate papers.   It may be stated here that gametophytic selection, as it affects the evolution of angiosperms, is a subject open to experimental study.   It is already apparent that the genetic result of this gametophytic selection is a matter of the first importance if it relates to some of the heritable characters,
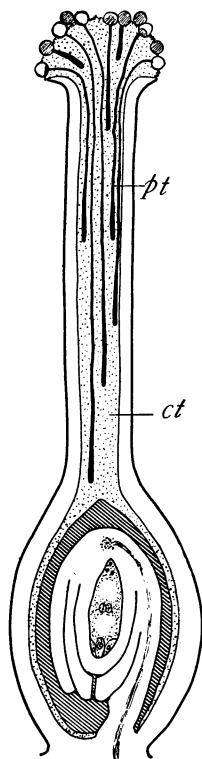
FIG. 28.—Diagram of pistil of angiosperm having one ovule, show-ing pollen tubes (*pt*) penetrating conducting tissue (*ct*) of style, en-gaged in competition to reach ovule, resulting in gametophytic selection.

especially in plants with long styles. While this pollen tube selection in angiosperms is morphologically very different from the embryonic selection in gymnosperms, it is physiologically a very similar process. In the case of the embryonic selection the embryo sporophytes are digesting their way and pushing forward into gametophytic tissue, while pollen tubes represent gametophytic structures penetrating sporophytic tissue by what appears to be a very similar method.

An important difference, however, between the gymnosperm embryonic selection and the pollen tube competition of angiosperms should be noted. The embryos concerned in the competition are diploid individuals, while the pollen tube and other forms of gametophytic competition take place between haploid individuals. The recent work of geneticists shows that lethal factors may be present in one member of a pair of chromosomes apparently without serious consequences, as long as the same lethal is not present at the same time in both chromosomes. Factors lethal to the gametophyte could not be protected in this way by a homologous chromosome.

INTEROVULAR AND INTERFLORAL SELECTION.—Another form of selection, belonging more or less completely to the categories of developmental selection, is that occurring in angiosperms between the ovules within the same ovary. In species of *Quercus*, for example, there are six ovules within the ovary, although normally only one ovule with one embryo is found developed in the acorn which matures from this ovary. In *Fraxinus* and in the olive there are two ovules in each pistil, yet only a single seed with one embryo is matured. There are numerous similar instances in the plant kingdom, and whether the elimination of the unsuccessful ovules in such cases occurs as early as the stage when the megaspores or female gametophytes are developing, or only among the ovules containing zygotes after fertilization has taken place, remains to be determined. According to the published accounts of the morphology, the latter is probably what happens in *Quercus*. The selection between reproductive organs during early vegetational stages, as that previously described for *Selaginella*, should be included in this category of developmental selection.

Interfloral selection is a form that may occur between the individual florets of a crowded inflorescence, such as the head of Compositae, the spike of maize, or the umbelled cluster of flowers in *Asclepias*. It is to be referred back to a struggle between the embryos contained in the different flowers, but since this competition is indirect, it is not usually very decisive. The process is less secluded from environmental influences, and takes on a form somewhat similar to the selection between vegetative branches described later. Interfloral selection is of little consequence in evolution as a form of developmental selection, except probably in rare instances.

VEGETATIVE FORMS OF DEVELOPMENTAL SELECTION.—Thus far the reproductional phases of developmental selection have been the chief concern. These reproductional types of selection are by far the most important, since through sexual reproduction new zygotes combining diverse hereditary strains come into existence. The developmental selection which takes place during reproduction, therefore, is a kind which may occur between different phenotypes, and produces results that are genetically very significant.

That there are also vegetative forms of this developmental selection process should not be overlooked, but this vegetative selection remains within the same genotype, unless a vegetative mutation occurs. For example, the branches of a tree are in a state of competition for light and favorable exposure. A struggle for development was suggested long ago by MÜLLER, who pointed out that there are many times more buds on every twig of a tree than can possibly develop into branches. While external circumstances of exposure may largely determine the result of this selection, the merits of the individual buds and their branches are also responsible in part for the result. If bud mutations occur, this vegetative selection determines at once whether they shall survive to reproduce themselves later or be eliminated. The principle is very largely the same for any form of vegetative selection, whether in gametophyte or sporophyte, by the dichotomy of thallus, aerial branches, stolons, tubers, rhizomes, or roots. When practiced for the purpose of obtaining vegetative mutation, bud selection has been called clonal selection. Of course, it is evident that this selection

does not belong rigidly to the categories of developmental selection, for it is subject very largely to external environmental conditions. It is not entirely in the external environment, however, since internal physiological correlations are concerned. It is clearly a type of selection standing between natural selection and developmental selection, as previously indicated.

Summary

Embryonic selection and gametic selection represent the important forms of developmental selection found among pteridophytes. Among gymnosperms the gametophytes plus the embryo usually take part in this competition, and among angiosperms it is typically a competition between male gametophytes represented by the pollen tubes. The important reproductive developmental process is merely shifted to an earlier stage of the life cycle in passing from ferns to angiosperms, where vegetative and other less important forms of developmental selection are also found.

Developmental selection in relation to natural selection and mutation

It is very evident that a good selective process, whether developmental, artificial, or natural selection is meant, should meet at least the following four requirements. It should (1) start the competition simultaneously, (2) take place under uniform conditions, (3) measure comparable merit, and (4) rigidly eliminate the great majority that fall below the standard.

First it should launch the individuals who participate into the competition with an even start. This is a primary requirement in any kind of a performance race. Well fitted is the process of fertilization to launch the competition of embryos, as this is a relatively sudden event, one which may happen only occasionally, and may be simultaneous in producing several or a large number of zygotes. Similarly the shedding of sperms from an antheridium provides an even start in the competition of sperms, with a definite goal to be reached through their activities. Pollination, especially when the pollen is transferred in masses or clumps by insects, is another more or less sudden event, which launches the competition

of pollen tubes. All of these events which start the various processes of developmental selection are superior or at least equal to the equivalent initiatory processes of natural or artificial selection. Among the latter seed germination which, while it gives a fairly even start to many of the competitors, is a more variable process, easily modified by soil conditions or delayed and unequal germination; it is slower and it is not usually as efficiently simultaneous as pollination or fertilization.

Selection between vegetative parts is also initiated by the awakening of the buds in the spring, a process which may be more or less simultaneous and comparable with seed germination under the most favorable conditions. Birth and the hatching of eggs in animals is a process well fitted to initiate the competition of natural selection. It is apparent that the processes of fertilization, pollination, and the liberation of sperms are all very superior means of beginning a selective process, and that there are only a limited number of these events in the life cycle of an individual.

The second requirement, that the competition should take place under uniform conditions, is one in which developmental selection excels, while natural selection is very inefficient. Under the conditions of isolation in pure culture in artificial selection, the environmental conditions are made very uniform, but even here the conditions are not as isolated and insulated as they are within the ovule of the pine seed, or within the tissues of the stigma and style, where pollen tubes must carry on their competition. On the other hand, the external environment where natural selection occurs is exceedingly complex and diverse.

The third requirement, that selection should measure equal merits, is also one in which natural selection falls far short of providing the best possible mechanism. In the external environment not all of the competing individuals which are "saved" are required to go through exactly the same performance, at the same time, in the same place, and under the same conditions. So many and varied are the factors that might be used to determine survival, and so different are the responses of plants that might be made to them in obtaining survival, that the capacity for an equal performance of the same task under similar conditions is not measured,

but rather a general indefinite all round fitness. It has already been shown, however, how developmental selection sets the same task for all the competitors. Likewise artificial selection sets a uniform standard of excellence of performance for all participants, but a standard which is limited by the powers of discrimination of the breeder.

By providing a very uniform medium for the competition of embryos, pollen tubes, etc., and by forcing rigid elimination, developmental selection precludes indiscriminate survival. The surviving plant may owe its existence to the performance record of its parent pollen tube, or it may owe its existence to its own performance during embryonic development; but in any event, there are very definite measures of some kind of excellence to be lived up to on a competitive basis. The surviving individuals constitute a class, selected for their superiority among several, among dozens, or even among hundreds of other individuals which were destroyed in this competition. Developmental selection, therefore, is not open to this objection which has been urged against natural selection.

In the fourth requirement, developmental selection again excels, while natural selection is only feebly effective, for the defeated individuals are rigidly eliminated in developmental selection. The losers in the environmental competition are not always destroyed from reproduction; their progeny may only be diminished somewhat. Artificial selection also meets this requirement fully.

In connection with these special features of developmental selection, it is interesting to consider some of the objections which have been raised against natural selection. One of these concerns the chances of death, which have been ably discussed by several evolutionists, who point out that the destruction of individuals is very indiscriminate, that the fittest do not always survive, for many of them are destroyed. Likewise, the least fit do not always perish. Thus it has been urged that there is little evidence that natural selection actually selects any specific class of individuals in preference to others. In fact, so complex is the environment in which natural selection must sort out the superior, that accident and chance really play a major rôle.

Another of the objections which have been urged against natural selection is that this theory rests altogether too largely on an unwarranted analogy with the process of artificial selection, although this supposed analogy was a very convincing argument in the hands of DARWIN. This analysis shows how natural selection is weak in at least three out of four of the requirements in which developmental selection excels, and how a much closer parallel or analogy may be drawn between developmental selection and artificial selection.

That there are many details which do not permit a close parallel between natural and artificial selection may further be illustrated. For example, the breeder in practicing mass selection, plants a large number of seeds in a uniform soil, and seeks to eliminate all other environmental differences wherever possible. Pure breeding in isolated cultures is possible, and at some definite stage when the seedlings come up, or as they mature, they may be measured and selected by very nearly the same standard of size and growth vigor, color, size of fruit, disease resistance, etc. Natural selection must necessarily be a much less methodical process. In nature, survival must be determined on the basis of a total or all round fitness. Very often this survival is purely fortuitous. Naturally disseminated seeds are less likely to germinate simultaneously in a uniform environment than planted seeds in a cultivated soil. If seedlings do not get an even start, are not growing in a uniform environment, are not measured up to the same standard, and the unselected are not always destroyed, survival by chance plays a very important rôle, and their apparent competition cannot be one of the greatest consequence. This has been urged as a very serious objection to natural selection even as a highly efficient selective mechanism, aside from the question of its power in originating species. Obviously the mechanism of developmental selection is much better fitted to bring about a competitive form of selection. It may be considered more efficient even than artificial selection, where uniformity of environment is only approximate, and the standards of selection depend upon the discriminative powers of the breeder. Finally, developmental selection makes possible a very early decision, which is doubtless a most valuable

form of biological economy, another feature in which developmental selection excels.

A further objection which has been made to natural selection has to do with the difficulties that are involved in explaining how the first steps in any given variation may be of selective value. How can natural selection influence a structure whose advantage is to be reached only at some future time, after the results of the selection are achieved? This is asking natural selection to pass on a prophecy. Developmental selection, however, is a form of selection which can act on some very small quantitative characters. For example, by playing on such features as minute differences in suspensor length and rate of growth in gymnosperms, or a rapid pollen tube penetration in seed plants, developmental selection brings about a positive selection for minute differences in these particular characters. It may be asked how this selection for embryonic or pollen tube vigor could in any way affect a selection for other characters. The answer is found in linkage of characters. A sporophyte character of the mature plant must be linked with the factors producing either vigorous suspensors and embryos, or vigorous pollen tubes in the gametophyte stage.

CORRENS found just such a case in *Melandrium*, which was referred to previously, in which the female-determining pollen tube has the quality of growing slightly faster than the male-determining pollen tube. Judging from his account, this linkage is probably not an exceedingly close one, as he states that there are some male-determining pollen tubes that grow faster than the slowest female-determining pollen tubes. Such a condition may be due to the well known crossing-over phenomenon associated with linkage, between the sex factor and the gene or genes producing rapid pollen tube growth. If factors affecting the rate of pollen tube growth should become linked with quantitative factors, which are usually multiple factors affecting the size of an organ or part, it is easy to understand how developmental selection can play on them indirectly through their linkages. An accumulation of the effect of this selection would account for the building of a new structure. Of course natural selection can also play on such a character or structure when it or a factor linked with it has become

distinctly useful or harmful to the organism, but not before the structure is present.

DARWIN recognized such linkage, calling it correlative variability. He accounted for many useless characters by assuming their linkage with other factors which are sufficiently useful to have a survival value. It has already been shown, however, that there is great difficulty in definitely pointing out that certain characters are actually acted upon in the environment by natural selection on a consistent basis. In developmental selection there is no doubt about a definite selection taking place, and the experimental evidence that certain adult sporophyte characters are linked with the gametophytic or embryonic factors having definite values in selection is also available.

This will also explain the production of overdeveloped structures, or those having no advantage to the organism. Suppose the factors determining the length or shape of the spines in the ends of some pine cone scales, or other useless details of the plant, should become linked with the genes producing either the most vigorous pollen tubes or embryos, there is no doubt that the selection for the pollen tubes or the embryos would result in the selection of the other characters in the same linkage. The spines would then be selected in or out, as the case may be, by developmental selection. Details of variations or mutations, be they ever so small, may either tend to disappear or become fixed or overdeveloped, as they are affected by this internal selective mechanism. Such phenomena of determinate variations and evolution in definite directions have long been recognized, and have been attributed to a principle called orthogenesis. The mechanism of developmental selection described here looks very promising as a means of accounting for many or thogenetic phenomena.

It is probably needless to point out that many characters would not be linked with these factors involved in developmental selection at all. These would remain unaffected by the developmental selection processes. Among these most of the heritable characters that have been studied by the Neo-Mendelians are to be found. The genes of these characters segregate independently of the factors affected by this selective mechanism, and yield Mendelian ratios in the expected proportions. Among those which should probably be

classed as the ones affected by some form of developmental selection are many of the lethal factors that have been described in some plants.   It has been shown by LITTLE that some kind of embryonic selection is responsible for the non-appearance of homozygous yellow mice whose inheritance was studied earlier by CUENOT. No attempt will be made to discuss here the lethal factors of *Drosophila* in this connection, but doubtless many things whose inheritance would follow the lethal type, could be caused by a kind of embryonic selection mechanism.

The origin of the variations or mutations is another problem. Chromosomal phenomena, such as gene mutations, the chromosomal mutation of non-disjunction, etc., are probably able to account for the actual origin of many variations.   Similarly bud mutations and other heritable vegetative variations would also be accounted for by some type of nuclear or intracellular phenomena.   They would be played upon by developmental selection even before their outward manifestations are recognized.   These mutations may also be acted upon by natural selection if they possess some very marked advantage or disadvantage.   It is in this connection that developmental selection has a very definite rôle in the origin and heritability of some mutations.   Only those variations which are not affected by developmental selection could reappear regularly or give consistent Mendelian results.   The outcome of developmental selection may be so decisively against a mutation that it may seldom recur.   On the other hand, if the mutation is closely linked with a factor greatly favored by developmental selection, it may reappear as if fixed, even though the pollen produced is heterozygous for it.   Thus we can understand how even the discovery and recognition of the mutations themselves depend upon whether they reappear in the next life cycle, and thus pass the censorship of the developmental selection machinery.   Developmental selection is doubtless responsible for the recognizability of some variations as mutations, but we have no evidence that it could be held responsible for the chromosomal phenomena themselves.

Summary

1. The process of developmental selection is a normal event or succession of events in the life cycle of vascular plants, where it

assumes various forms, being represented chiefly by embryonic selection, gametophytic selection, and gametic selection.

2. Developmental selection differs materially from natural selection, germinal selection, the intraselection of ROUX, as well as the other selection theories.

3. Records of conspicuous cases of polyembryony in ferns are brought together. Original studies are added, constituting definite evidence that a selective plurality of embryos may normally exist even in the leptosporangiate ferns. Nearly all living ferns seem to have embryonic selection, or show evidence of having passed through a stage in which embryonic selection was the normal condition. The embryonic selection represented by the poly-embryony of gymnosperms was derived from an embryonic selection habit in their fern ancestors.

4. Developmental selection in gymnosperms and angiosperms is not only represented by a selection among embryos, but also by a selection between female gametophytes and the male gameto-phytes represented by the pollen tubes.

5. A form of selection intermediate between natural selection and developmental selection may be recognized in the competition between buds and branches of a sporophyte or a branching thallus.

6. Developmental selection is a process which brings into play a definite internal competition between embryonic diploid individuals, as well as between the haploid sperms of fern plants, and the haploid male and female gametophytes of gymnosperms and angiosperms. On the other hand, natural selection usually acts on the diploid generation in these plant groups, or on the haploid fern gametophytes, where selection may take place in the external environment.

7. The discussion seeks to show why the process of developmental selection is not open to the more serious objections which have been urged against natural selection, and on what basis it equals or excels the latter as an effective selective process.

8. The discussion also shows how developmental selection may account for some of the phenomena of orthogenesis on a mechanical basis.

9. Developmental selection is not responsible for the origin of the chromosomal or other intracellular phenomena involved in

mutation, but it is a powerful mechanism whose censorship may determine whether or not any particular intracellular phenomena causing mutation may complete the life cycle to be heritable, and therefore recognizable as a mutation.

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